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A PRELIMINARY STUDY OF THE BREEDING BIOLOGY OF THE SPRUCE GROUSE IN NORTHWESTERN MONTANA

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B.S. University of British Columbia, 1964

Presented in partial fulfillment of the requirements for the degree of

Master of Science in Wildlife Technology

UNIVERSITY OF MONTANA

1967

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". . . the less one knows, the longer it takes to explain what little one knows. Yet I will try to make clear what I think I know. . ."

Niko Tinbergen (1961)

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ACKNOWLEDGMENTS

I wish to extend my gratitude to all individuals who assisted me during this study.

I am grateful to my supervisor, Dr. R. S. Hoffmann, for his valuable advice and criticisms of the manuscript. I am also indebted to the members of my advisory committee: Dr. P. L. Wright, Dr. D. A. Jenni, and Dr. W. L. Pengelly, for their many helpful suggestions. Dr. I. Hjorth, Institute of Zoology, University of Uppsala, Sweden, criticised parts of the thesis and T. W. Mussehl, Montana Fish and Game Department, offered many valuable suggestions.

Special thanks are extended to N. A. M. Verbeek and to Dr. C. J. Jonkel for their help during the initial stages of the study. I am also grateful to Dave and Jo Lynne Whitmer, Big Creek Ranger Station, for their generous assistance while I was in the field. Dr. F. C. Zwickel gave me a dog (English pointer) who proved to be indispensable to the study. Dr. R. Plakke provided me with fall specimens.

I am grateful to the Montana Cooperative Wildlife Research Unit[1] for providing financial assistance, to Dr. J. J. Craighead, Unit Leader, Gerry Atwell, Mrs. Alvina Barclay, and to the other members of the Wildlife Unit, for their encouragement and advice.

I also wish to thank the personnel of the Montana Fish and Game Department, Kalispell, Montana, of the Glacier View Ranger Station, Columbia Falls, Montana, and of the Polebridge Ranger Station, Glacier National Park, Montana, for their cooperation.

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[1] Fish and Wildlife Service, U. S. Department of the Interior, Montana Fish and Game Department, University of Montana, and the Wildlife Management Institute cooperating.

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INTRODUCTION

The spruce grouse (*Canachites canadensis* L.) occurs throughout the boreal forest life zone of North America (Aldrich and Duvall, 1955; Aldrich, 1963), from the Maritime Provinces to British Columbia and Alaska. The northern limit of their range is tree line and in the east they occur as far south as northern Wisconsin, Michigan and Minnesota. In the west, they follow the Rocky Mountains into western Montana and Idaho.

Bent (1932: 120), Brooks and Swarth (1925: 48) and other early workers, classified the spruce grouse into two species. The first, *Canachites canadensis*, was further split into four subspecies: *C. c. canadensis* occurring throughout Canada, *C. c. osgoodi* found in central Alaska, *C. c. canace* found around the Great Lakes, and *C. c. atratus* of the coastal region of south-eastern Alaska. Aldrich (1963), however, only recognizes three of these subspecies as he includes *C. c. osgoodi* with *C. c. canadensis*.

The second species named by early workers was the spruce grouse of the Rocky Mountains, called Franklin's grouse (*Canachites franklini*). Bent (1932) suggested, and Aldrich and Duvall (1955) confirmed, that the characters of the Franklin's grouse overlap with those of the spruce grouse where the two ranges come into contact. For this reason, the latter authors consider the Franklin's grouse a subspecies of the spruce grouse (*C. c. franklinii*).

In Montana *C. c. franklinii* are found in the northwest mountainous areas (Wright and Hiatt, 1943a: 18; Craig, 1959). Wright and Hiatt

(1943a) claimed these birds were abundant only in Lincoln, part of Flathead and a small part of Glacier counties. A modern census of the tetraonid populations of Montana is lacking, hence, the present range of C. c. franklinii may differ from what it was thought to be in 1943.

"The spruce grouse is second only to the ruffed grouse in the extent of its geographic range, but it has the smallest literature of any American tetraonid" (Hamerstrom and Hamerstrom, 1963). To my knowledge, only seven scientific papers other than taxonomic studies have been published dealing solely with this grouse. Three of these cover food habits (Jonkel and Greer, 1963; Crichton, 1963; Ellison, 1966) and one is on behavior (Lumsden, 1961a). Lumsden and Weeden (1963) published notes on the harvest of these birds, Ammann (1963) discussed their status in Michigan, and one paper described a spruce-blue grouse hybrid (Jollie, 1955). Interest in these birds, however, has increased since the Hamerstrom's review. At present, W. R. Robinson is conducting a field study in Michigan, L. N. Ellison is working in Alaska, and D. A. Boag is directing research on these birds in Alberta (personal communications).

The purpose of this investigation was to study the breeding biology of a spruce grouse population in Montana. Since information on this species is extremely scarce, it was necessary to conduct a general, preliminary study. As a result, information on any one aspect was limited. However, the data from this study should help to orient future investigations.

In 1965, the field work was begun on April 17 and was terminated on August 30. In 1966, I was on the study area from April 15 until August 30.

STUDY AREA

Location and Physiography

A suitable study area was located in the Flathead National Forest approximately 7 miles south of Polebridge, and 30 miles north of Columbia Falls, Montana, on the west side of the North Fork of the Flathead River at the mouth of Coal Creek (Fig. 1).

The area was bounded on the north and west by Coal Creek and on the east by the North Fork spur road. The southern boundary was trail number 310 (Fig. 2). The size of the area thus bounded was approximately 600 acres.

The elevation of the plot was roughly 3500 feet; topographically it was flat with a gentle downward slope (2-3 degrees) to the east.

The north and west boundaries were marked by sheer banks, 75-100 feet in height, cut by Coal Creek. Two intermittent stream beds traversed the plot from west to east but these did not markedly affect the topography of the area. During the spring, snowmelt filled these beds but they soon dried up. However, small ponds along one of them persisted until mid-June. By July, in the absence of heavy rains, no standing or running water remained on the area.

Weather

The area lies in the Pacific (Northwest) storm track, and therefore the climate is greatly modified by oceanic influences. Due to the prevailing westerly winds which bring moisture-laden air into the region, the annual precipitation is much greater than the average for Montana (Hawley, 1955).

Figure 1. Map showing general location of the study (not to scale).

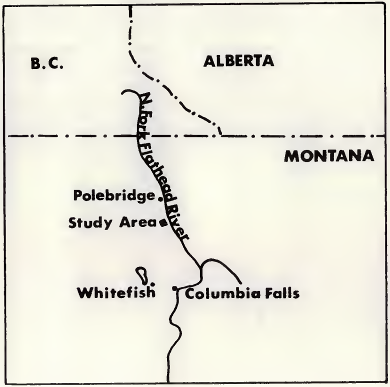
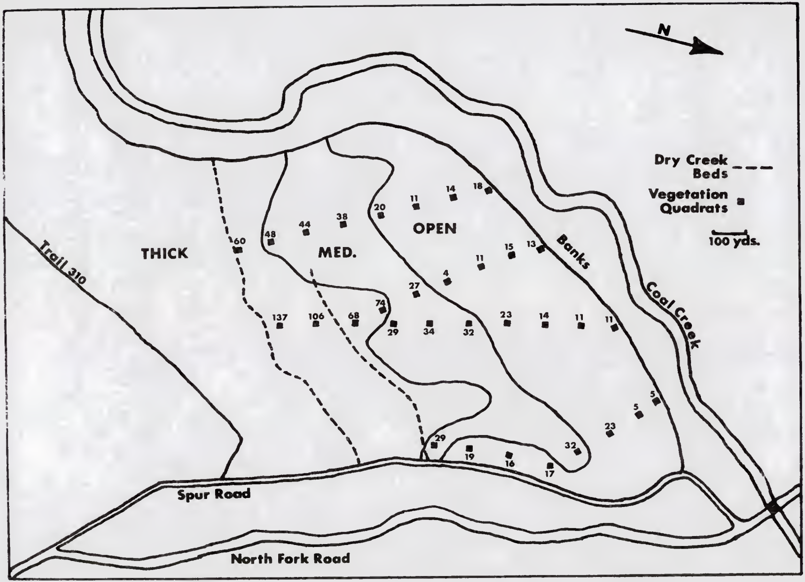

B.C.
ALBERTA
MONTANA
N. Fork Flathead River
Polebridge
Study Area
Whitefish
Columbia Falls

Figure 2. Map of the study area showing vegetation zones. The numbers at each quadrat are the number of trees per acre (x 100).

Figure 3. Daily maximum and minimum temperatures for April and May measured at the study area.


N
Dry Creek Beds
Vegetation Quadrats
100 yds.
THICK
MED.
OPEN
Trail 310
Banks
Coal Creek
Spur Road
North Fork Road
18
14
11
20
38
44
48
60
15
13
11
4
27
74
137
106
68
29
34
32
23
14
11
11
5
5
23
32
29
19
16
17

A weather station was set up in the forest adjacent to the study area. Temperature one foot above the ground was recorded on a 7-day thermograph, and accumulated precipitation was measured once a week. In addition to this station, climatological data recorded at Polebridge, Montana (7 miles north of the study area), were available (U. S. Department of Commerce, Weather Bureau, and Dightman, 1961).

A comparison of the two sources of data shows discrepancies that could be attributed to the location of the stations, one in the forest, the other in the open. Generally, the average maximum temperatures were higher at Polebridge and the minimum temperatures were lower. Precipitation on the study area was not measured with standard equipment and is useful only for comparison between years and not with the data collected at Polebridge.

The air temperature, during the period of the study, varied from a high of 86 (August 8 and 9, 1965) to a low of 7 degrees F (April 18, 1966). Daily maximum and minimum temperatures are shown in Figures 3, 4, 5, and 6. Daily temperature fluctuations were greater in April 1965 than in April 1966 (Fig. 3). This was probably due to the greater snow depths present in 1965 (see below). At the end of April the maximum temperatures were much higher in 1965 than in 1966. In the first part of May, however, the situation was reversed. These large fluctuations of maximum temperatures, both daily and between years, continued throughout May and June. July temperatures, however, were more consistent both between days and between years (Fig. 5). In August, maximum temperatures fluctuated greatly between days but were relatively consistent between the years (Fig. 6). In both years there was a general decline in the temperature towards the end of this month.

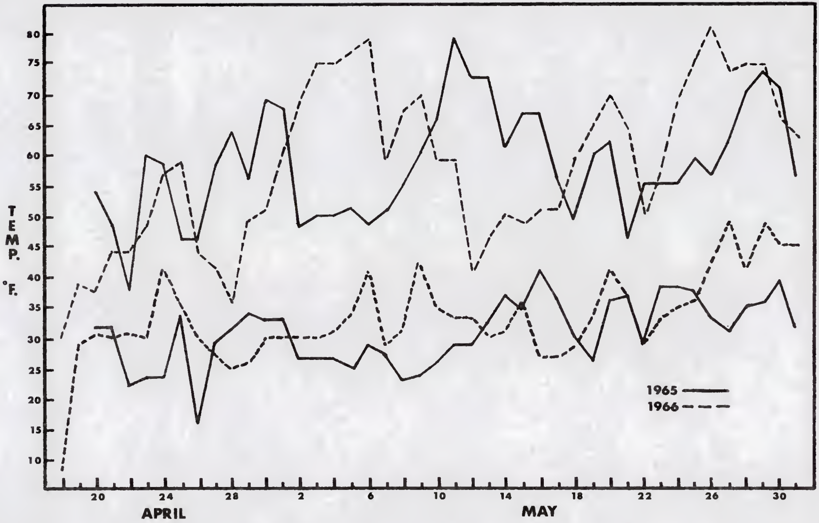

80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
TEMP.
°F.
20
24
28
2
6
10
14
18
22
26
30
APRIL
MAY
1965
1966

Figure 4. Daily maximum and minimum temperatures for June.

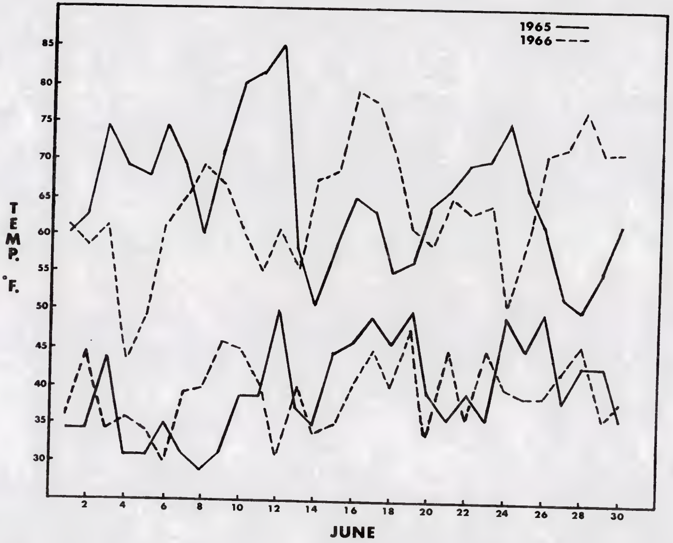
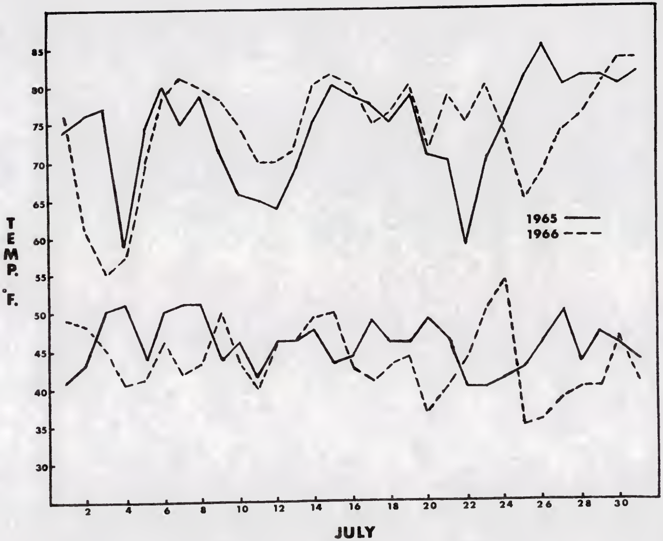

1965 ——
1966 - - -
TEMP. °F.
85
80
75
70
65
60
55
50
45
40
35
30
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
JUNE

Figure 5. Daily maximum and minimum temperatures for July.


85
80
75
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55
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45
40
35
30
TEMP.
°F.
1965
1966
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4
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8
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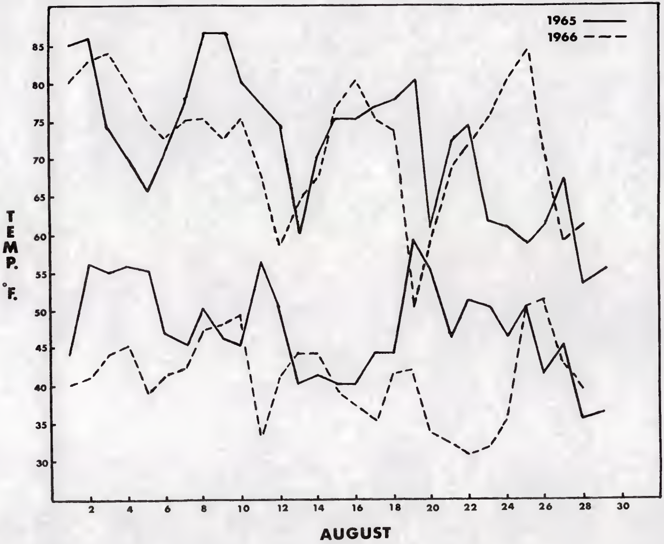
20
22
24
26
28
30
JULY

Figure 6. Daily maximum and minimum temperatures for August.


1965
1966
85
80
75
70
65
60
55
50
45
40
35
30
TEMP.
°F.
2
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22
24
26
28
30
AUGUST

On April 19, 1965, 23 inches of snow was measured on the ground at the study area. This continued to decrease until only patches were left by the first of May. When I arrived in 1966 (April 17), only 2 to 3 inches of snow covered the ground. This was reduced to small scattered patches by April 25 and was completely gone by May 1.

Precipitation data (Figs. 7 and 8, and Table 1), from both sources, show that 1966 was generally a wetter year than 1965. The month of August was the only exception. In both years June was the wettest month. The data for May, July and August suggest that they were comparable to one another. However, in May, much of the rain fell during the daylight hours while evening thundershowers accounted for most of the precipitation recorded for July and August.

Table 1. Number of days on which .01 inches or more precipitation was recorded at the Polebridge weather station.

Year	May	June	July	August
1965	8	15	8	11
1966	10	21	6	7

On June 4, 1966, a storm that passed through the area produced a very heavy snowfall (approximately 8 inches). This storm caused a great deal of damage, particularly to the deciduous vegetation. The study area, however, was only mildly affected.

Vegetation

The vegetation zone of the general area is Engelmann spruce (Picea engelmanni) - subalpine fir (Abies lasiocarpa) (Daubenmire, 1952). A

Figure 7. Monthly precipitation data from the Polebridge weather station.

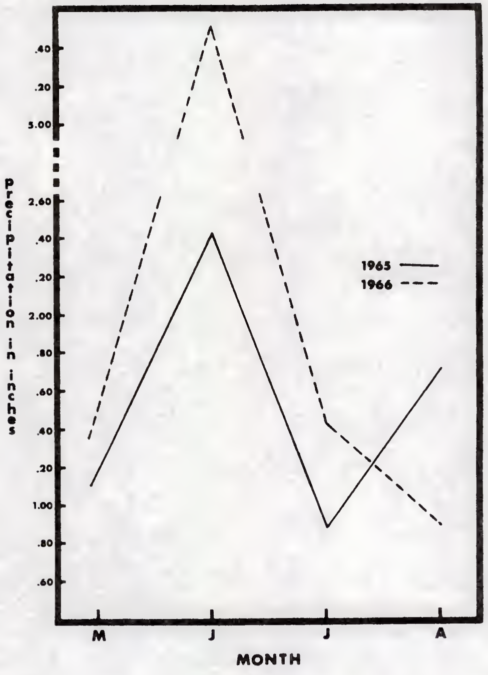
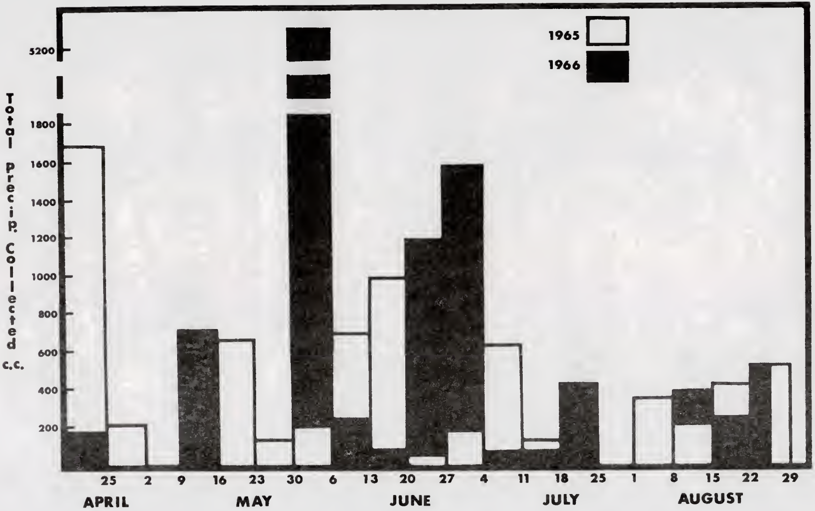

precipitation in inches
.40
.20
3.00
2.60
.40
.20
2.00
.80
.60
.40
.20
1.00
.80
.60
M
J
J
A
MONTH
1965
1966

Figure 8. Weekly precipitation data, given as total amount collected, measured at the study area.


1965
1966
Total precip. Collected c.c.
5200
1800
1600
1400
1200
1000
800
600
400
200
25
2
9
16
23
30
6
13
20
27
4
11
18
25
1
8
15
22
29
APRIL
MAY
JUNE
JULY
AUGUST

number of fires, however, have removed these climax species on large tracts of land. On many of these burned areas, including the study area, the lodgepole pine (Pinus contorta) is the dominant species. At present, the lodgepole pine is mature, with spruce, subalpine fir and, to a lesser extent, western larch (Larix occidentalis) making up the understory. The subalpine fir and Engelmann spruce were between 1 and 6 feet in height, while the larch were generally taller, 10-15 feet. No young lodgepole pine were found on the area.

The lodgepole pine on the area was divided into three zones, according to tree density, open, medium and thick (p. 23; Figs. 2, 12, 13, 14). The species of shrubs varied with the density of the lodgepole pine. Buffalo-berry (Shepherdia canadensis) and huckleberry (Vaccinium spp.) were found mainly in the 'open' zone. Snowberry (Symphoricarpos rivularis) was dominant in the 'medium' zone and shared dominance with thimbleberry (Rubus parviflorus) in the 'thick' zone. Common bearberry (Arctostaphylas uva-ursi) and mountain lover (Pachistima myrsinites) were found in all tree densities.

The ground was covered by herbs, grasses (Gramineae) and mosses (Musci). The occurrence of the herbs varied as the season progressed. Following snowmelt the ground vegetation consisted of evergreen shrubs, Prince's pine (Chimaphila umbellata) and mosses. Wake robins (Trillium ovatum), dogtooth violets (Erythronium grandiflorum) and fairy slippers (Calypso bulbosa) were the first annuals to make an appearance. These were later replaced by lupine (Lupinus spp.), arnica (Arnica spp.) and beargrass (Xerophyllum tenax) which persisted as the dominant herbs through most of the breeding season. Herbs were more abundant in the

less-dense lodgepole pine. In the 'thick' zone, grasses and mosses were often the dominant ground vegetation.

Fauna

The general region in which the study area is located supports a large and varied assortment of animals (Bailey and Bailey, 1918; Lechleitner, 1955; Parratt, 1964). The lodgepole pine forest, however, has a depauperate fauna.

No attempt was made to quantitatively or qualitatively sample the animals. Chance sightings, during the course of the two summers, were reduced due to the presence of the dog. This was particularly evident for the carnivorous mammals known to occur in the area. Identification of passerine birds was also extremely difficult due to the density of the forest.

Mammals. Large mammals seen on the area were: elk (*Cervus canadensis*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and black bear (*Ursus americanus*). The cervids did not appear to be resident on the area and were seen mainly in the spring. On the other hand, the study area did appear to be a part of a black bear's range. Smaller mammals included red squirrels (*Tamiasciurus hudsonicus*), Columbian ground squirrels (*Citellus columbianus*), chipmunks (*Eutamias* spp.), and snowshoe hare (*Lepus americanus*). The red squirrels were numerous throughout the area. Ground squirrels, however, were limited to openings and to the less dense forest. Grouse often used the dirt from a ground squirrel's tunnel for a dust bath.

Birds. The bird fauna of the area was poor in both number of

species and number of individuals. Birds known to be nesting on the area included the Oregon junco (*Junco oreganus*), gray jay (*Perisoreus canadensis*), chipping sparrow (*Spizella passerina*), and Swainson's thrush (*Hylocichla ustulata*). Chickadees were also numerous, particularly in early spring. The black-capped (*Parus atricapillus*) and mountain (*Parus gambeli*) chickadeed were most common. Occasionally boreal (*Parus hudsonicus*) and chestnut-backed (*Parus rufescens*) chickadees were seen. Other birds, notably warblers, were heard on the area but were never seen.

Grouse. Three species of grouse were present in the general area; spruce, ruffed (*Bonasa umbellus*), and blue (*Dendragapus obscurus*). During the reproductive season, however, these are separated by habitat requirements. Blue grouse were limited to open, south-facing slopes, above 4000 feet, ruffed grouse were mainly in the deciduous forest along creek beds, and spruce grouse were restricted to the coniferous forest. Blue grouse were found in the forest adjacent to the open parkland but spruce grouse were never found in the open. Ruffed grouse occurred in all forest types but also were never found in the open.

Only spruce and ruffed grouse resided on the study area during the breeding season. The ruffed grouse were found along the edges and in pockets of deciduous vegetation. Occasionally they were located in the lodgepole pine forest occupied by spruce grouse. In 1965, a female ruffed grouse successfully hatched a clutch of eggs in an area which, the following year, was occupied by a spruce grouse brood. In all, two ruffed grouse nests (both in 1965) and one drumming male were located on the study area. Although none of these birds were banded, others were sighted that were probably either transients or from adjacent areas.

METHODS

Locating Grouse

Finding the grouse proved to be extremely difficult due to the density of the vegetation and to the fact that they spent much of their time in the trees. For this reason, a dog (English pointer) was used constantly (Fig. 9). He proved to be indispensable to the study as he accounted for over 95 percent of the sightings. However, a number of difficulties were encountered in working the dog in this type of cover.

This breed, and closely related ones, are noted for their speed and their ability to cover a large amount of ground in a short period of time. While this is advantageous when working in open cover, it presented a problem on my study area. Due to the density of the vegetation the dog was out of sight much of the time. This was overcome by attaching a bell to his collar. The breed is also noted for their ability to 'point' the birds. This was also a problem as I was unable to locate him while he was on 'point'. I overcame this obstacle by not reinforcing the pointing behavior. Hence, the dog flushed the grouse as soon as they began walking away. The birds generally flew up into trees, not far (30 feet) from the flushing site. The dog would then begin searching in the immediate area. The localized sound of his bell would attract me and I was able to locate the grouse in most instances. In addition, the dog howled if he saw the grouse in the tree.

A final problem was the dog's long tail, which, particularly during periods of excitement (as when he located a bird), he wagged wildly.

After several weeks of smashing it on the trees, the tip began to bleed. To prevent this I bandaged and put splints on his tail.

Birds in trees, not flushed by the dog, were extremely difficult to locate. Once again the dog proved indispensable to the study. Although he rarely located the birds, he would spend a great deal of time searching in the immediate area. Once again the localized sound of his bell attracted me and, in most cases, I was able to find the grouse.

In essence, a workable solution to the problem of locating the birds, under these adverse conditions, was the combination of my dog's specialized skills and my learning how to work with him.

The area was walked in a random pattern allowing the dog to direct the search.

The finding of chicks was accomplished without the aid of the dog. Chicks less than one week old stayed on the ground and were very difficult to locate. The problem was compounded by the hen, as she stayed in the vicinity and clucked constantly. Chicks older than one week generally flushed into trees, but were only slightly easier to find.

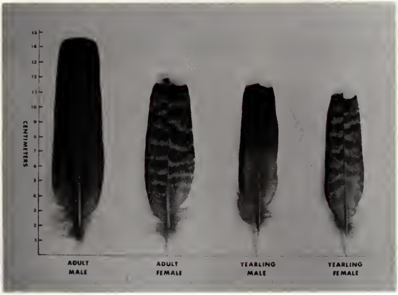
Catching Grouse

The birds were 'noosed' in the manner described by Zwickel and Bendell (1967). The equipment consisted of a slip noose on the end of a 20-foot, telescopic, fiberglass pole. The noose, roughly 4 inches in diameter and made of plastic-coated nylon, was placed over the bird's head and tightened around its neck (Fig. 10). All birds were noosed out of trees. Birds that were too high to catch were flushed by shaking the tree in which they were sitting. They generally flew only a short distance (20 yards) and would land in another tree, often at a lower height.

Figure 9. The dog 'pointing' a spruce grouse which is sitting in a tree. Note the bell attached to the dog's collar.

Figure 10. Noose (arrow) passing over the head of a ruffed grouse.

Figure 11. Central rectrix from each age and sex class of spruce grouse.


CENTIMETERS
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
ADULT MALE
ADULT FEMALE
YEARLING MALE
YEARLING FEMALE

Two noosing fatalities resulted from the grouse falling off the limbs on the wrong side. In one case, the bird's jugular vein was severed and in the other the neck was broken. In a normal noosing, however, damage and feather loss was slight.

Chicks, after they reached flying age, were also caught with the noose.

Handling Grouse

Marking. Captured birds were individually marked with numbered aluminum leg bands (size no. 4) in combination with colored (red, yellow, blue, and green), plastic bandettes (size no. 5). Each bird, therefore, carried one aluminum band and one or two plastic bandettes on its legs. One bird, banded as a yearling in 1965, was recaptured in 1966 with extensive leg damage caused by a bandette being too tight. The bands were removed and placed on the healthy leg. The bird survived and was last seen on the area on August 26.

Sexing and aging. The sex and age of each bird was recorded. No problems were experienced in sexing the birds, as the plumages are sexually dimorphic. The spring and early summer population was divided into two age classes: adults and subadults, or yearlings. Adults were birds two years old and older while yearlings were birds hatched in the previous year. The primary remiges were used to divide the birds into these two classes. The two outer primaries (9 and 10) are not lost during the postjuvenile molt (Wright and Hiatt, 1943b). These two juvenile feathers are more pointed and often of a lighter color than the new adult ones. In the first postnuptial molt, one year later, all primaries are replaced

and this difference is lost. This criterion, however, was not always reliable for aging C. c. franklinii, as the difference in the appearance of the primaries was often very slight. Primaries 8 and 9, from one wing of each bird captured, were pulled and saved. This permitted a check on the age at a later date.

Lumsden and Weeden (1963) suggested the use of length and color of the central rectrix as a means of sexing spruce grouse. I found the birds could easily be sexed using the color of this feather. The male rectrix lacked the distinct brown barring characteristic of the female rectrix.

In addition, it was noted that this feather could be used to determine age (Fig. 11). A comparison of the total lengths of the removed center rectrices in the two age classes is given in Table 2.

Table 2. Length of the central rectrix.

Age and Sex	No. of Birds	Average Length (mm)	Range (mm)
Adult Males	12	145	138-148
Yearling Males	5	118	114-128
Adult Females	10	120	117-125
Yearling Females	6	108	103-115

These data correspond with that presented by Lumsden and Weeden (1963): males, 122-148 mm.; females, 108-119 mm.

The color of this feather was also useful for aging the birds. The central rectrix of the adult male is generally solid black, although some had a light brown flecking in the lower half. In the yearling male

this feather has a white terminal band and a varying amount of light brown speckling. The difference between the age classes in females is more subtle. While the color pattern remains the same, the feather has a faded appearance in the yearling. Conversely, the colors are darker and richer in the adult.

Both primaries and rectices were used in determining the age of most birds. In comparing the methods, the use of tail feathers was found to be faster and more accurate. One female had two center tail feathers of different types. One had the coloration of a yearling and was 109 mm. long, the other resembled an adult in color and was 115 mm. long. The primaries suggested that this bird was a subadult.

Since primaries 9 and 10 are molted at a later date than the rectrices, the wing is the only aging criteria available in late summer.

General. All captured birds were also checked for molt, brood patch and any unusual external features. The cloacal temperature was taken and the bird was weighed with a spring balance. It was then released.

No bird was damaged due to handling and none appeared to suffer any ill effects. All either flew or walked away from the banding site.

Each banding site was marked with a $1\frac{1}{2}$-foot length of 3-inch wide plastic. The bird's band number was written on the plastic which was then fastened to a tree. In addition, a small patch of bark was peeled from the tree and the band number was written on the exposed wood with a grease pencil. These served two purposes: first, the exact banding site could be relocated at a later date and, secondly, they were used as landmarks for tying-in grouse sightings.

Observing Grouse

Banded birds resighted during the course of the study were generally not renoosed. The birds were identified by their bands and the locations were ascertained as accurately as possible.

A blind was used when birds were observed for any length of time. This consisted of a 6 by 8 feet piece of green cloth which was hung on the trees. The blind, however, was not always effective. During the mating season, the birds would not begin displaying in my presence even when I was behind the blind. This was overcome by placing a mounted skin in a male's display territory and then moving away some 50 to 60 yards. After a wait of roughly 5 minutes I slowly approached and was able to observe the displays.

The density of the vegetation made observations under any circumstances extremely difficult. In order to keep the bird in view, I had to stay so close that they always appeared to be aware of my presence.

Vegetation Sampling

The lodgepole pine was sampled by 10-yard square quadrats spaced 100 paces apart along a north-south compass line. Four lines were run across the area. Due to the homogeneity of the area and to the lack of landmarks, the plots were not connected by a true compass line. The result was unevenly spaced, crooked lines (see Fig. 2). However, I do not think this affected the sampling. In all, 32 quadrats were established on the area.

The corner trees of each quadrat were marked with pieces of brightly colored surveyor's tape and the line and quadrat numbers were written on them. Hence, the quadrats also functioned as landmarks.

The trees contained in the quadrats were counted, measured and marked. The measurements included circumference (at belt height), and estimates of total height and the distance between the ground and the beginning of the needles. Each tree was chipped with an axe after it was recorded to prevent errors in counting.

The number of stems per acre varied from 436 to over 13,000 (Table 3). In general, the density of the trees increased from north to south. Variations from this generality (eg., line 3, quadrat 4) were due to tongues and patches of more open forest in the denser areas. Small openings (up to 20 feet square) also reduced the number of trees in some of the quadrats.

The mean circumference of the trees in the quadrats (Table 4) decreased as the density increased. By comparing Tables 3 and 4 it is possible to distinguish between areas of evenly spaced, large trees and dense areas with many openings (both having the same number of trees per quadrat). An example of this is a comparison between line 1 quadrat 8 and line 2 quadrat 7. In the first case, openings were present while in the second, the trees were larger.

The study area can be roughly divided into three zones according to tree density (Fig. 2). The zones, open, medium and thick, were broad bands which traversed the area from southwest to northeast. The density in the 'open' zone (Fig. 12) did not exceed 2500 trees per acre. The 'medium' zone (Fig. 13) varied from 2500 to 5000 trees per acre and the 'thick' zone (Fig. 14) contained densities of over 5000 trees per acre. A fourth possible zone, 'very thick' (densities over 10,000), existed between the southern dry creek bed and trail 310.

Table 3. Number of trees per acre per quadrat.

Line No. East → West	Quadrat No. North → South									
	1	2	3	4	5	6	7	8	9	10
1	532	532	2275	3194	1694	1646	1936	2856		
2	1065	1113	1355	2275	3243	3388	2856	6776	10648	13746
3	1307	1452	1113	436	2710	7357				
4	1791	1404	1065	2033	3824	4404	4840	6002		

Table 4. Mean circumference of trees per quadrat (inches).

Line No. East → West	Quadrat No. North → South									
	1	2	3	4	5	6	7	8	9	10
1	18.6	21.3	11.4	8.5	12.8	12.5	9.9	8.1		
2	17.1	16.3	16.1	11.4	9.8	9.9	12.0	6.7	6.1	5.0
3	17.1	15.7	11.5	19.1	14.7	8.2				
4	15.0	16.3	14.8	11.7	8.5	9.6	7.7	7.9		

Figure 12. Photograph representing the 'open' vegetation zone.

Figure 13. Photograph representing the 'medium' vegetation zone.

Figure 14. Photograph representing the 'thick' vegetation zone.

The mean of the estimated height of the trees in the quadrats generally varied with the circumference. The mean heights ranged from 50 to 20 feet. The average estimated distance between the ground and the needles, however, varied only slightly with the size of the trees. The extremes in the quadrats were a maximum mean of 34 and a minimum mean of 15 feet. In the majority (24 of 32) of the quadrats the mean distance from ground to needles ranged from 20 to 30 feet.

The relationship between the size and density of the lodgepole pine and the grouse will be discussed in the section on population dynamics.

An attempt to use these quadrats for sampling the understory conifers (pine, spruce and larch) failed due to the lack of an adequate sample of these species.

POPULATION DYNAMICS

Numbers

Resident population. In 1965, four adult males and three adult females were caught and banded on the 600 acre study area. This appeared to constitute the entire resident breeding population. Evidence that these birds were residents include localized movements (p. 30) and frequency of resighting (Table 5). In 1966, the resident population was ascertained with more certainty when previously banded birds were relocated in the same specific area. Of the seven grouse thought to be residents in 1965, six were relocated in 1966, but one, banded as a yearling in 1965, appeared as a new resident. While this replacement maintained the number of resident birds, the sex ratio changed since the bird lost was a female and the one gained was a male.

In both years the resident spring population was composed of adult birds only and all adults were residents.

Transient population. In the two years of the study a number of birds were found on the area that did not appear to be residents. In all cases these were yearlings (Fig. 17). The fact that most of these birds were only seen once or twice indicates that they were transient. Only two of the five yearlings banded in 1965 were relocated the following year. One was 2½ miles from her banding site and the other had taken up residence on the area.

Table 5. Number of sightings made on banded birds.

Bird No.	Year Banded	Sex	Age	No. of Sightings		
				1965	1966	Total
601**	65	M	Ad.	1	-	1
602*	65	M	Ad.	9	28	37
603	65	M	Yrlg.	2	-	2
604*	65	M	Ad.	10	17	27
605	65	M	Yrlg.	1	-	1
606*	65	F	Ad.	11	26	37
607*	65	F	Ad.	9	-	9
608*	65	F	Ad.	3	7	10
609*	65	M	Ad.	2	6	8
610	65	F	Yrlg.	1	1	2
611*	65	M	Ad.	6	7	13
612	65	F	Yrlg.	1	-	1
613*	65	M	Yrlg.	2	21	23
614**	66	F	Ad.	-	1	1
615**	66	M	Ad.	-	1	1
616	66	F	Yrlg.	-	1	1
617	66	M	Yrlg.	-	3	3
618	66	F	Yrlg.	-	3	3
619**	66	F	Ad.	-	1	1
620**	66	F	Ad.	-	1	1

* Resident birds.
** Banded off the study area.

Movements

When banded birds were encountered, their locations were recorded as accurately as possible. Due to the homogeneity of the vegetation exact locations were not always obtained. This was particularly true for the early part of 1965, when I was unfamiliar with the area. However, since the magnitude of the possible error was relatively small, it is trivial compared to the map scale.

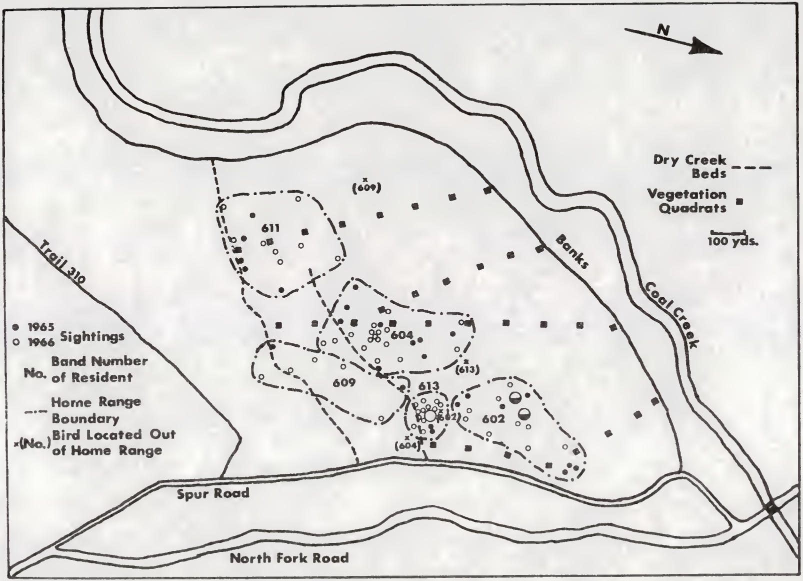
Birds located in the early part of the 1965 field season were unbanded and are not included in the data.

Resident males. Sightings of resident males during the two years are plotted in Figure 15. The data definitely show that these birds restricted their movements to localized areas, and that they used the same areas each year. Hypothetical boundaries drawn around the sightings (Fig. 15) enclose what can be called 'home ranges'. The spatial arrangement of the enclosed areas further suggests that these are home ranges. The existence of territories within the home ranges was not ascertained with any certainty. However, evidence will be presented for individual birds suggesting that they do have territories.

Bird number 602 was seen a total of 37 times (Table 5) during the two years. All but one of these sightings was in an area of approximately 10 acres. The bird, however, utilized some parts of this area much more extensively than others. During the 1966 display period (April 25-May 21), the male was located in a small area (30 yards square) 9 out of 11 times. It appears that this small area constituted a breeding territory. Immediately following this period he moved south-west 50 yards and was seen repeatedly at this new location. In all, these two small areas (totaling not more than one acre) accounted for 75 percent of the sightings in 1966. In 1965, fewer sightings were obtained but 50 percent of them were in the same two small areas. In 1966, this bird was seen once 50-60 yards south of his home range. This was the only recorded instance of one territorial male occurring in the home range of another male. At this time 602 was with a female (606) and the territory holder (613) was located 30 yards away.

During the two years of the study, male 604 occurred in an area of approximately 15 acres. This bird, however, was less localized than

Figure 15. Map of the distribution and movements of resident males. The dashed line encloses the home range of each bird and the large circles represent 10 or more sightings at the same place.


N
Dry Creek Beds
Vegetation Quadrats
100 yds.
Banks
Coal Creek
Trail 310
● 1965
○ 1966 Sightings
No. Band Number of Resident
Home Range Boundary
x(No.) Bird Located Out of Home Range
611
604
609
613
602
(609)
(613)
(604)
602
Spur Road
North Fork Road

602 and frequented a greater portion of his home range. Since few sightings were made on 604 during the display period, I was unable to determine the extent of his territory. In 1965, he was seen approximately 200 yards east of his home range in an area that was unoccupied at the time. Like 602, he was accompanied by a female when found outside of his home range.

Male number 611 occupied a 10-acre home range in the south-western portion of the study area. Although this bird was only seen 13 times, he was never found outside of this general area.

Bird 609 was seen the least of all the resident males. However, he appeared to occupy a home range between the two dry creek beds. On one occasion this bird was located on his home range and 4 days later he was relocated in the western corner of the study area 700 yards away. In 2 days he was again seen on his home range.

Male 613 was first located and banded as a yearling late in 1965. In 1966, he was relocated in the same area and remained there for the duration of the study. This new home range, however, was established in a formerly unoccupied area and did not appear to disturb the boundaries of adjacent home ranges. During the period of display, he was repeatedly sighted in a quarter-acre area. This further supports the theory that these birds hold territories in early spring. This bird, however, remained close to his territory for the remainder of the study and occupied a home range of only 3 acres. On one occasion he was sighted 150 yards west of his range in an area not occupied by resident males.

The data in Figure 15 suggest that each of the resident males is restricted to a home range and that males occupied territories, particularly during early spring (April and May), within their home ranges.

Since these birds rarely occurred outside of their boundaries, the restriction is probably a social rather than a physical one. There appears, however, to be an upper limit to the size of a home range. This was shown by the movement of one male, during the period of the study, into an unoccupied area. This suggests that the spaces between existing home ranges are actually unoccupied territories and the general area could probably maintain a higher male population, were there not other limiting factors.

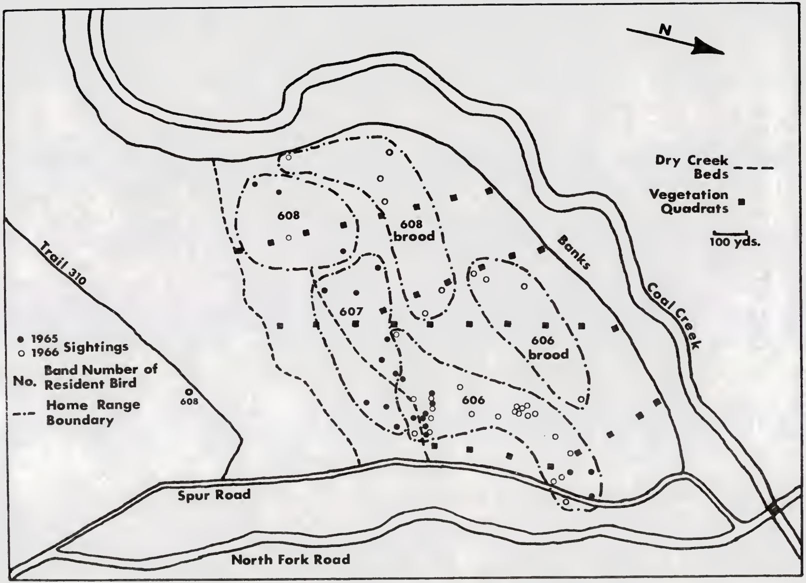
Resident females. The observations of resident female birds are plotted on Figure 16. These data show that females are also restricted to specific areas. Although these areas were in contact, hens were never found in another's area. This information suggests that the females also occupied home ranges. The spatial arrangement of the 1965 home ranges was remarkably similar to the home ranges of three of the resident males (611, 604, and 602).

Female number 607 occupied a home range in 1965 but was not relocated in 1966. This hen resided in the same general area as male 604 but only once were these two birds seen together. This female did not produce a brood.

In both years hen number 608 occupied the same region as male 611. This bird was broodless in 1965 but successfully raised a brood in 1966. Although few sightings were made when she was broodless, the data suggest that a different area was used when with a brood. The brood moved extensively throughout its range and was last seen 700 yards south-east of this area.

In 1965, female 606 was broodless and occupied an area adjacent

Figure 16. Map showing the distribution of resident female home and brood ranges.


N
Dry Creek Beds
Vegetation Quadrats
100 yds.
Trail 310
Banks
Coal Creek
608
608 brood
607
606 brood
606
608
● 1965
○ 1966 Sightings
No. Band Number of Resident Bird
Home Range Boundary
Spur Road
North Fork Road

to male 602. However, she was seen with this bird only once. Female 606 was seen most frequently in an area not occupied by males. In 1966, she was first relocated in this same area which was now occupied by male 613. She then moved across her range and remained on or near 602's territory during the mating season. On June 14, presumably while nesting, she was found in the north-east corner of her home range. She was first located with a brood on July 8 in a previously unoccupied area to the north-west. She then moved 400 yards south-west and remained in this area until she lost her brood on July 13. Following this, she moved east to the road and then south to male 613's home range. She then appeared on 602's home range and was seen repeatedly thereafter with him. On one occasion, late in the season, she was located with male 604 on his home range. This was the only instance where one of the resident females invaded the general area vacated by the missing hen 607.

In 1966, an unbanded yearling female was sighted several times on the home range vacated by 607. Although I was unable to capture her, her unusual wild behavior indicated that she was the same bird. I was forced to collect her in order to determine her age. It was noted that no other females moved into the area after she was removed.

Resident broodless females appeared to occupy home ranges that were coincidental with those of resident males. Although the females moved more extensively and occupied greater areas than the males, there also appeared to be an upper limit on the size of their ranges.

Hens with broods occurred in areas distinct from their general home ranges. The major difference between the two areas was the vegetation (p. 39). The three females occupied almost all of the available habitat in 1965 and the loss of one of them the following year did not

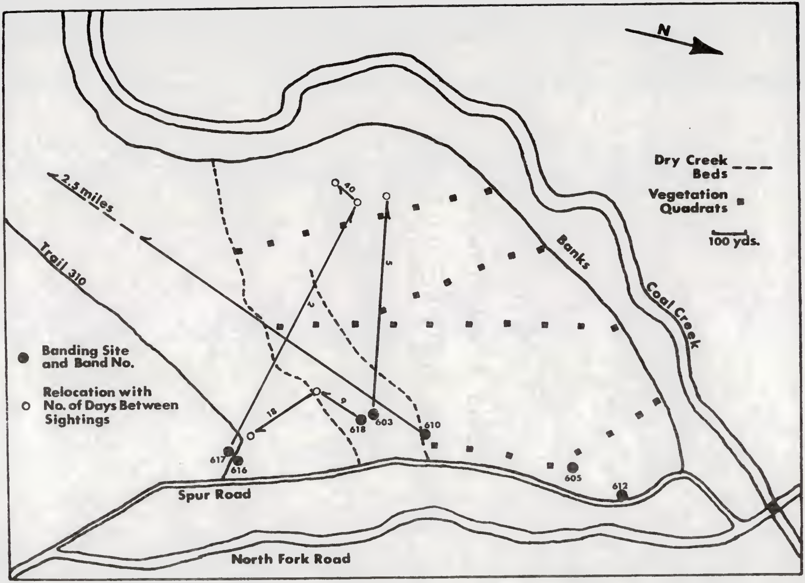
alter the ranges of those remaining. This suggests the study area had a maximum female population in 1965 and that an increase in numbers might be accompanied by a reduction in the size of the existing home ranges.

Yearlings. Other than the two cases previously cited (male 613 and unbanded female), no yearling birds appeared to be resident on the study area. All yearlings were banded along the eastern edge of the study area (Fig. 17). Three of these birds were seen only once. One male (603) was resighted 5 days later approximately 600 yards west of where he was banded. A second male (617) also moved west 750 yards in only 2 days. This bird, however, was found 40 days later only 100 yards from his second sighting. Since this area was not occupied by a male and the last sighting was in late August, it is possible that this bird will be a 1967 resident on the area.

The longest straight line distance measured between sightings was recorded for female 610. She was banded on the study area in 1965. In 1966, she was relocated on a ridge approximately 2½ miles south and over 1000 feet above her banding site. At the other extreme, female 618 traveled only 100 yards in 9 days and 200 yards in the next 18 days. It is possible that this bird may also become a future territory holder.

The data suggest that yearling birds of both sexes traveled extensively during the early part of the breeding season. Late in the season, however, they restricted their movements to unoccupied areas, over-wintered, and if they appeared the following spring, it was as territorial adults. If this is true, then the breeding population on the study area may increase.

Figure 17. Map of the distribution and movements of yearling birds. The lines depict the distance covered, the arrow represents direction and the number is the number of days between sightings.


N
Dry Creek Beds
Vegetation Quadrats
100 yds.
2.5 miles
40
5
2
Banks
Trail 310
Coal Creek
● Banding Site and Band No.
○ Relocation with No. of Days Between Sightings
9
18
618
603
610
617
616
605
612
Spur Road
North Fork Road

Habitat Selection

Males. Resident males occupied home ranges that were in 'medium' and 'thick' lodgepole pine (see vegetation, p. 23, and Figs. 2, 12, 13, 14). All but two of the ranges (609 and 613) contained parts of both zones. Both of these were in the 'thick' zone but the enclosed dry creek beds provided narrow bands of less dense forest.

The males were never found in the 'open' zone. The home range of bird 602 was bounded on the east by this zone. On three separate occasions he was located near this boundary but in each case he flushed into the thicker cover. The avoidance of this zone by these birds could be related to their requirement of the trees for food and cover. It was observed that the needles were only present on the upper one-third of the trees. In the 'open' zone the trees were larger, hence, the available needles (near the trunk) were higher than in the other two zones. In addition, the branches were progressively smaller and more brittle below the level of the needles. The birds' problem then is threefold. First, they would have to fly greater distances to reach food. These birds, however, did not exhibit any tendencies to perform long flights. Second, they would have difficulty perching on the lower branches, and third, they would be more easily detected against the bare tree trunk.

The 'medium' zone was occupied by males 602 and 604 during the early part of the reproductive season. Males 611 and 613 utilized areas along the dry creek beds during this period. Immediately following the mating season (approximately May 25), males 602, 604, and 613 moved into the 'thick' zone of their territories. They remained in this zone for the duration of the breeding season and were seen only

occasionally back in the 'medium' zone. Male 611 appeared to be the only exception to this movement. However, the density of the lodgepole pine into which he moved (4400-4800 trees per acre) is very close to what I have arbitrarily designated as 'thick'.

No attempt was made to analyse the microhabitat of these birds because most sightings were made after they had been flushed by the dog. Since the habitat can change abruptly within a short distance, the results would have been biased in many cases.

Females. Broodless adult females occupied roughly the same habitat as the resident males. They moved extensively throughout their ranges without apparent preference for the 'thick' or 'medium' zones but generally avoided the 'open' zone. Female 606, however, was frequently found along the border of a patch of mixed deciduous and coniferous trees which was also adjacent to the 'open' forest.

The only birds that occupied the 'open' zone were brood hens 606 and 608. Hen 606 first appeared with her brood close to the junction between the 'medium' and 'open' zones. She then moved well into the 'open' zone and remained there until she lost her brood. Following this she returned to the habitat she occupied prior to nesting. Female 608 and her brood were also first located just inside the 'open' zone. She remained in this area until late July at which time she moved into the 'medium' zone. She was last sighted in mid-August across the area in the 'thick' zone.

The ground vegetation in the 'open' was much more dense than in the other zones. It was also noted that Vaccinium sp. berries were present only in this region. Therefore, these hens, in bringing off

their broods on or near this area, could make use of this source of food. By the end of July, the chicks were capable of longer flight, hence, their dependency on ground vegetation was reduced. They then moved into the thicker lodgepole pine which provided better protection from predation.

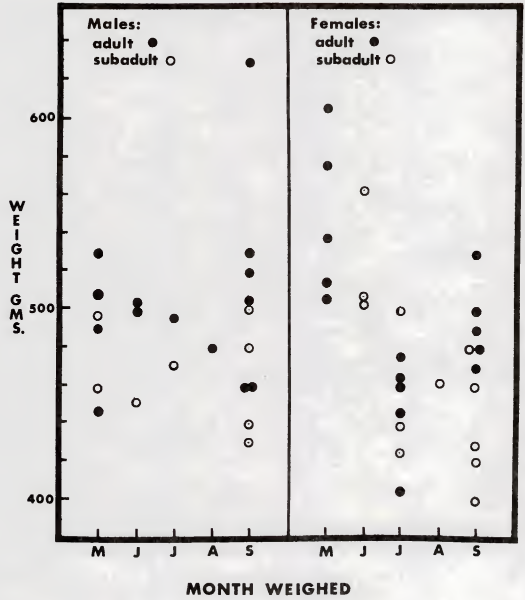
Individual Growth

Weight. Bendell (1955) found that the weights of adult male blue grouse did not change significantly while on the spring-summer range (April to September). Although my data are insufficient for statistical analysis, Figure 18 shows that there was no weight change trend for the adult male spruce grouse. Fourteen adult males, weighed from May to September, averaged 501 grams with extremes of 630 and 446 grams.

Yearling males likewise showed no seasonal weight change. Data from young of the year, weighed in September, were comparable to yearlings weighed earlier in the season. Four yearlings averaged 466 grams and varied from 450 to 496 grams. The September juvenile males averaged 462 grams and varied from 430 to 500 grams. This indicates that juvenile males gained very little or no weight over their first winter.

Five adult females weighed in May had a greater mean weight (548 grams, range 506-606 grams) than five adult females weighed in July (450 grams, range 405-476 grams). As suggested by Bendell (1955), this was probably due to the presence of eggs and is, therefore, of little significance. Five adult hens weighed in September had a mean of 494 grams (range, 470-530 grams) which suggests the birds were gaining weight after breeding activities and prior to winter.

Figure 18. Monthly weights of spruce grouse recorded from May to September. Note the subadult birds weighed in September are juveniles in the first fall of life.


Males:
adult ●
subadult ○
Females:
adult ●
subadult ○
WEIGHT GMS.
600
500
400
M
J
J
A
S
M
J
J
A
S
MONTH WEIGHED

Three yearling females weighed in June averaged 518 grams (range, 505-563 grams) which was similar to the adult females weighed in May. The mean yearling weights for July (455 grams) and August (462 grams) also closely paralleled the mean July weights for the adult females. This implies that yearling females were producing eggs. Five juvenile females weighed in September averaged 438 grams (range, 400-480 grams) which indicates these birds gained weight over the winter.

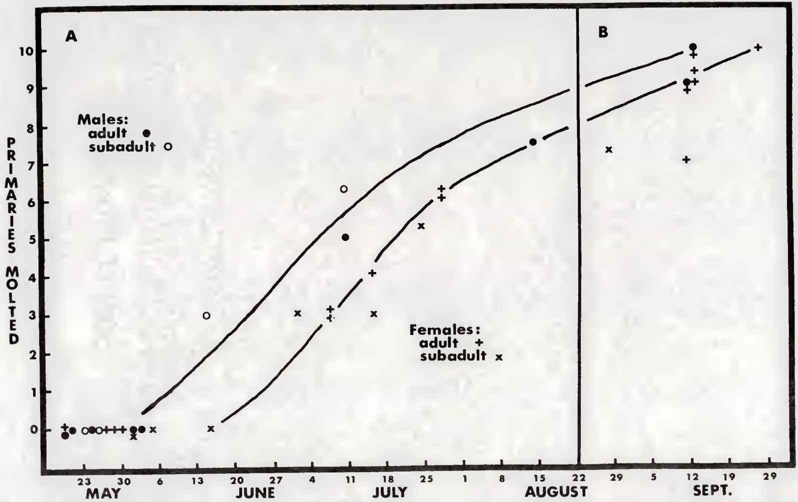
Molt. Since most birds were handled prior to the commencement of molt, data on this were extremely limited.

Bendell (1955) stated that on Vancouver Island adult and yearling blue grouse of both sexes began molting by the last week of May. Boag (1965), who worked with blue grouse in south-western Alberta, found that adult males and non-breeding subadults of both sexes commenced the molt approximately 4 weeks in advance of adult females and breeding subadult females.

Spruce grouse in this study commenced the molt of their primaries around the first of June (Fig. 19). The data suggest that males of both age classes began molting one or two weeks prior to adult and subadult females. Data from birds taken in various localities in Montana during September suggest that the primary molt is usually completed by the third week of this month.

Boag's data indicate that the primaries are dropped at one week intervals up to the sixth feather. The last four feathers, however, are lost at a decreased rate. By extrapolation, I have completed hypothetical primary loss curves for both sexes (Fig. 19).

Figure 19. Primary molt curves for male and female spruce grouse.


A
B
PRIMARIES MOLTED
0
1
2
3
4
5
6
7
8
9
10
Males:
adult ●
subadult ○
Females:
adult +
subadult x
23
30
6
13
20
27
4
11
18
25
1
8
15
22
29
5
12
19
29
MAY
JUNE
JULY
AUGUST
SEPT.

Replacement of the rectrices began after the second week of July. The sequence of feather loss, however, was variable. In the normal pattern the outer feathers were dropped first and the molt proceeded toward the center. In a number of cases, however, all rectrices were lost at the same time. One adult male was observed on July 6 with what appeared to be a complete tail. On July 15 all rectrices were gone and no new ones were visible. By August 1, the feathers were all one-half grown in and by August 15 the tail again appeared to be full.

Most birds checked in September had completed the replacement of their rectrices. Occasionally, however, females showed an incomplete molt at this time, suggesting that the molt of nesting females is retarded.

Chicks. Data for chick growth are lacking due to the fact that only two broods were located on the area. When caught, the chicks were weighed and their primaries measured using the method outlined by Zwickel and Lance (1966).

The gain in weight by the chicks is shown in Figure 20. While most of the chicks weighed were from one brood, the weight of a chick from another brood fits the curve. This indicates that the two broods were hatched at approximately the same time.

Growth and molt of primaries is shown in Table 6. Since the date of hatching is unknown it is impossible to correlate primary growth with age. The data suggest that chicks completed their postjuvenile primary molt by the end of September.

Figure 20. Growth curve for spruce grouse chicks. The closed dots represent chicks from brood 608 while the open dot represents a chick from brood 606.

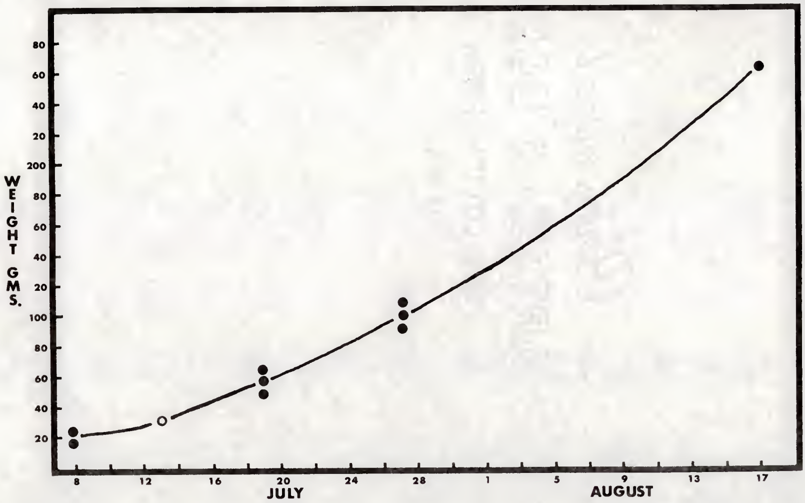

WEIGHT GMS.
80
60
40
20
200
80
60
40
20
100
80
60
40
20
8
12
16
20
24
28
1
5
9
13
17
JULY
AUGUST

Table 6. Growth and replacement of juvenile and postjuvenile primaries.

Date (No. of Birds)	Primary Number*									
	1	2	3	4	5	6	7	8	9	10
July 8 (2)	40	42	43	44	46	42	36			
July 13 (1)	F1	F1	47	49	50	46	41	22		
July 19 (3)	P	F1	F1	F1	F1	65	58	36		
July 27 (3)	1/2	1/4	P	F1	F1	F1	F1	64	18	P
Aug. 17 (1)	F2	F2	F2	F2	7/8	1/4	F1	F1	95	64
Aug. 28 (2)	F2	F2	F2	F2	F2	1/2	1/4	F1	F1	3/4
Sept. 12**	F2	F2	F2	F2	F2	F2	2/3	F1	F1	F1
Sept. 12**	F2	F2	F2	F2	F2	F2	F2	7/8	F1	F1
Sept. 24 (2)	F2	F2	F2	F2	F2	F2	F2	F2	F1	F1

* Juvenile primaries measured in mm.
Postjuvenile primary growth estimated in relation to full grown feather (1/8, 1/4, 1/3, 1/2, 2/3, 3/4, and 7/8).
P - represents a new feather in which the vane has not yet broken from the quill.
F1 - represents full grown juvenile primaries.
F2 - represents full grown postjuvenile primaries.

** Extremes of 13 birds examined on this date.

Food Habits

The limited number of grouse in the area prevented regular collections for food habit study. Jonkel and Greer (1963) analysed 56 Franklin's grouse crops collected in the fall, over a 3-year period, from the general vicinity of the study area. They found the predominant food item, during the fall, was western larch (Larix occidentalis) needles. The larch needles, however, were only available until October. At this

time the consumption of pine (Pinus spp.) and spruce (Picea engelmanni) needles and the fruit of white mandarin (Streptopus amplexifolius) increased. Crichton (1963) reported similar findings for the fall and winter food habits of the central Ontario spruce grouse. The crops collected in the fall contained mainly jackpine (Pinus banksiana) and tamarack (Larix laricina) needles and to a lesser extent blueberry (Vaccinium angustifolium) leaves. The winter diet of the Ontario spruce grouse consisted almost entirely of jackpine needles. Ellison (1966) examined crops of Alaskan spruce grouse and also found that the diet varied according to the season. In spring (April or May and June) the birds primarily ate spruce (Picea spp.) needles and the leaves and buds of various Vaccinium species. In summer (July and August) the predominant food items were Vaccinium spp. leaves and berries and crowberries (Empetrum nigrum). Very few needles were taken in the summer. By early September (fall), however, spruce needles were taken along with the summer foods. In late fall (October) the diet consisted mainly of spruce needles and lesser amounts of Vaccinium berries and leaves. The winter food of the Alaskan spruce grouse consisted almost entirely of spruce needles.

The grouse of my study were observed eating lodgepole pine (Pinus contorta) needles throughout April, May and June. The latest these birds were observed eating needles was June 30. The crop of one female, collected on May 5, contained only lodgepole pine needles. Examinations of winter and spring droppings indicated that conifers were the main diet item during these periods.

The crop of a female collected on July 1 contained only snowberry (Symphoricarpos rivularis) leaves. Observations of the ground vegetation

revealed that grouse preferred mountain lover (Pachistima myrsinites), bearberry (Arctostaphylos uva-ursi) and snowberry leaves. One female, collected on July 15, had one bearberry, 9 Vaccinium spp. berries, one ant (Hymenoptera) and one moss (Musci) capsule in her crop. On July 28, a female's crop contained only pieces of unidentified fungi (Basidiomycetes).

These isolated observations suggest that the food habits of these birds followed the trends suggested by other workers. The late fall, winter and early spring diet consisted almost entirely of lodgepole pine and other conifer needles while herbaceous vegetation and insects were utilized during the summer months.

Predation

In the two years of the study only two instances of grouse predation were recorded. One was a ruffed grouse nest that was completely destroyed and the other was a ruffed grouse adult of which only the feathers and feet were left. Both of these were along the eastern boundary in the mixed coniferous-deciduous forest and in both instances the predator was unknown.

Throughout its range the spruce grouse is popularly known as the 'fool hen'. This is due to their reluctance to fly and to their apparent lack of fear of man. In the two years of the study, however, only one resident bird did not return to her territory the second year and may have been killed by a predator.

The lack of predation was probably due to the density of the vegetation (p. 23) and to the behavior of the birds (p. 72). Avian predators, both day and night hunters, probably have trouble in locating

the grouse through the lodgepole pine canopy and in flying through the maze of stems. The birds were extremely wary when on the ground and avoided ground predators by flushing. This was exemplified by the dog (a trained ground predator) who was never able to catch an adult bird on the study area. They further escaped detection by flying some distance and then circling back, landing in a tree and remaining motionless. Arboreal predators would have problems in climbing the straight, small branched lodgepole pine without being detected. I observed that birds would flush if branches near them or the whole tree were shaken.

The chicks, however, appear to be vulnerable to predation. In the open habitat they are more susceptible to avian predators. The tendency to scatter when disturbed, their cryptic coloration and their ability to freeze, probably all help to reduce their chances of being caught by a ground predator. The hen's behavior (p. 66) also aids the chicks. Once they are old enough to fly, they can escape by flushing into trees. However, their reluctance to fly out of the tree when disturbed makes them more vulnerable to arboreal predators, such as martin (Martes americana).

The critical period for the spruce grouse appears to be their first summer and fall. Since the chicks in the fall are somewhat less wary than the adults, this could lead to some winter predation. Birds surviving to the following spring, in the right habitat, have a good chance of surviving for a number of years.

BEHAVIOR

Introduction

The behavior of C. c. franklinii was studied during its reproductive season. This study, however, was primarily concerned with learning the birds' habits and, therefore, descriptions of their behavior are incomplete.

The behavioral patterns have been divided into two main groups, reproductive and maintenance. Reproductive behaviors include breeding, nesting and brooding. Since no natural grouse interactions were observed during the breeding season, mounted study skins were used. A reproductively active male gave a different response to a female study skin than to a male skin. Descriptions of these are under the headings of courtship and aggressive displays.

Maintenance behavior includes patterns not directly associated with reproduction, but patterns mainly concerned with the survival of the individual.

A. Reproductive Behavior

The breeding season is that period when behavior associated with mating was performed. Three displays were observed during this period. The first was a flight display, the presence of which delineated the breeding season. The other two (courtship and aggression) were elicited through the use of mounted skins.

Flight Display

Description. In this display C. c. franklinii showed the greatest variation from the other sub-species of spruce grouse. A careful comparison of the two displays, however, shows that in spite of the apparent differences, there are many similarities.

Lumsden (1961a) described the flight display of the Ontario spruce grouse as follows:

> The descent from the tree to the snow drift or the ground was always carried out in a characteristic manner. The bird flew down steeply, but apparently normally, until about four to six feet above the ground. The body was then swung into an almost vertical position, the tail fully spread, and the bird descended on rapidly beating wings very steeply to the ground. . . .

C. c. franklinii performed the same basic display, but with the following difference. Having checked the downward flight and assumed a vertical position, the bird then dropped straight to the ground producing two loud sounds. These are best described as resembling two loud claps. I was unable to determine what mechanisms were involved in producing these sounds, but one biologist working on C. c. franklinii (MacDonald, personal communication) has evidence that the wings are involved. Hence, the display has been called 'wing-clapping'.

This display appears to be homologous to the 'flutter-jump' described by Lumsden (1961a). Hjorth (personal communication) prefers to call the spruce grouse display a drumming flight and claims that the wing-clap is a specialization of this.

The starting point of the display was either a limb on a standing tree or the trunk of a bent tree. The height above the ground usually varied from 10 to 15 feet. However, on a number of occasions, birds were flushed from the ground into trees at heights of up to 40 feet. The birds wing-clapped as they flew to the ground from these heights.

No intention movements were observed prior to the wing-clap display which differed from those prior to normal flight. On occasion, the birds assumed a mild strutting posture similar to sexual display (to be described later) but this could not be classed as preflight behavior. In the normal flight display the bird's feathers were unruffled and the eye combs were only one-half inflated.

The flight to the ground was as described by Lumsden (1961a). In one instance the bird flew downward normally but when it was approximately 2 feet above the ground, it turned towards the direction from which it had come (180 degrees), gained from 2 to 3 feet in altitude, then dropped to the ground and produced the characteristic clapping sounds. In only one instance was a bird observed wing-clapping and landing in another tree rather than on the ground. This unusual behavior could have been caused by my presence.

In all but two of over 45 flight displays recorded, the number of clapping sounds per display was two. On both those occasions only one sound was heard. The birds were not observed displaying in either case so no reasons can be given for these variations.

Occurrence of flight display. In 1965, wing-clapping display was first heard on May 19 and was not heard after May 25. In 1966, this display began on April 25 and continued until May 21.

Because of my unfamiliarity with both the area and the birds, wing-clap display could have begun earlier in 1965 than the date recorded. The week of May 19 through May 25 was the peak of breeding activity.

During the mating season, birds under observation were active, feeding, walking on limbs, and flying to other trees and to the ground. Conversely, at other times during the study they sat quietly in a tree

and often remained there for many hours. Thus, the termination of display was readily ascertained.

The sequence of behavior was observed much more closely during 1966. On April 25, one resident male performed a wing-clap display twice. Two days later, I observed markings in fresh snow that suggested a bird had been displaying. The location was on the territory of the bird observed wing-clapping earlier. On April 29, while watching a male, I heard another bird wing-clap. There was no response from the bird I was watching. On May 2, I approached a known territory and heard the bird begin wing-clap displays. The bird on the adjacent area also began to display. No displaying was heard again until the 13th of May. From this date until May 21 wing-clapping was frequent.

Table 7. Comparison of the extreme temperatures on days with and days without wing-clap display during the mating season.

	Maximum (F)			Minimum (F)		
	High	Low	Average	High	Low	Average
With display	64	41	54.1	38	22	31.0
Without display	77	41	60.5	43	29	39.4

Although peaks of display occurred both early in the morning (roughly one-half hour before to one-half hour after sunrise) and in the evening (a half hour before to a half hour after sunset), birds were frequently heard wing-clapping during the middle of the day.

The data suggest that weather influences the birds during the period of display. As shown in Table 7, birds tended to wing-clap on cooler days. The temperature at the time of display varied from a high

of 59 to a low of 32 with an average of 43.9 degrees F. During both years the termination of display was coincidental with a rise in the daily maximum temperature. On three occasions the percent cloud cover was zero. For the other 11 recorded periods of flight displays the cloud cover varied from 50 to 100 percent. Precipitation did not appear to affect the birds as they were observed displaying in the rain. It is probable, however, that severe rain or snow storms inhibited their activity.

The data suggest that the occurrence of flight display is controlled by a number of factors. Besides the internal state of the bird and a disturbance stimulus from the environment, the temperature, cloud cover, and time of day also appear to have an effect.

If other conditions were favorable, the birds often responded to my presence (a disturbance in their environment), with a wing-clap display. It is possible, therefore, that the frequency of this display might be quite different in an undisturbed situation.

Display sites. Four banded adult males were observed displaying during the 1966 breeding season. The birds were spatially arranged so that their home ranges did not overlap (see Fig. 15). Two of the birds were very localized during the display period which suggests they held display territories. One of the other two birds utilized several specific sites within a 25-yard radius. The last male moved extensively and did not appear to use specific sites. The latter, however, was the only male that did not have a female on or adjacent to his home range. In 1965, a female occupied this range and an unbanded male (presumably the same bird) did use specific sites for the wing-clap display. All birds

however, wing-clapped outside of their territories if disturbed; however, they remained within their home range boundaries.

Three of the males displayed in small openings (20 feet square) in the dense forest. The other male's territory was in the less dense forest. When wing-clapping, birds used the trees on the periphery or bent trees in the center as take-off points and the openings for landing.

Hooting. On several occasions, but only during the breeding season, a vocalization, attributed to C. c. franklinii, was heard. This consisted of a very low frequency 'hoot'. The number of hoots in a sequence varied from one to four. At no time was a bird observed hooting and, to my knowledge, no written account of a hooting spruce grouse exists. Therefore, the importance and function of hooting during the mating season is unknown. Hjorth (personal communication), however, is of the opinion that it is an incomplete threat that has been ritualized. This display appears to be more common during the early phases of the breeding period.

Discussion.

> With the possible exception of two North American species, the Sage Grouse (Centrocercus urophasianus) of the plains and the Ruffed Grouse (Bonasa umbellus) of forests, the males of all Grouse perform an aerial display, the function of which is advertisement of territory (Lumsden, 1961b).

The Hamerstroms (1960) found for the Greater Prairie chicken (Tympanuchus cupido pinnatus) that the 'flutter-jump' display was a response to the movements or vocalizations of other birds, and also attracted other birds to the display ground.

The wing-clap display of C. c. franklinii appears to be in response to an external stimulus. From the discussion on movements (p. 29)

these birds can be considered territorial. This display, therefore, probably also functions as territorial advertisement. However, a more plausible explanation would be that it functions to advertise the internal reproductive state of the bird. In this context, although no evidence is available, it probably serves to attract females.

The birds during this period of activity responded to being disturbed, either by me or my dog, with a wing-clap display. The birds also responded to the wing-clapping of other birds. Yearling males on the periphery of a display area and mounted study skins in the center of the area did not elicit a flutter-jump response. In one case the resident male appeared after a yearling had been captured on the edge of his territory. Following release, the yearling flew out of sight and the adult flew back to the center of his territory. If the male was in a tree when a study skin was placed in his area he wing-clapped as he flew down to it. However, he also wing-clapped if there was no study skin and if he was on the ground when presented with the skin he did not perform a flight display.

From the preceding discussion, the functions of this display appear to be numerous as do the stimuli eliciting it.

Courtship Displays

On two occasions (May 16 and 18, 1966) a male displayed to a mounted female skin. The response has been divided into a number of postures and movements.

Strutting. The strutting posture of C. c. franklinii is the same as described by Lumsden (1961a) for the Ontario spruce grouse (Figs. 21 and 22). The strutting discussed here is the high-intensity strutting

display performed in the proximity of the female during the mating season. The strutting postures in response to my presence and those performed after mating will be discussed later.

In high-intensity strutting, the eye combs were very large and red, the tail was elevated to just below the perpendicular (70 degrees) and was partially opened, the undertail coverts were spread and drooped in layers, the overtail coverts were spread, the primary remiges were slightly drooped, the lower breast feathers were erected and pointed forward, the upper breast feathers and the feathers on the front of the neck were erected and pointed upwards, and the feathers on the chin were fluffed. The bird's body was held horizontal, with the head elevated and slightly forward. The normal shape of the neck was lost due to the upturned feathers which increased its width. When viewed head-on, the appearance was one of two bright red combs set against a black background. The background was supplied by the neck and the tail. A solid white line on the breast delineating the neck patch was also visible. The upper and under tail coverts combined to produce a dashed white circle around the tail.

Tail movements. Throughout the courtship display the rectrices were constantly moving in the vertical plane. For clarity, I have divided the movements into two types: tail-fanning and tail-flicking.

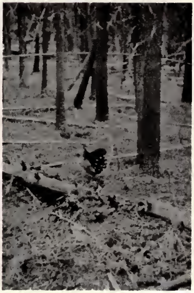
In tail-fanning, the rectrices were held just below the perpendicular and were spread symmetrically from a one-quarter to a three-quarter open position. This movement was performed rapidly with only a slight pause in the open position. Tail-flicking involved a movement of both the whole tail and the rectrices. The tail, starting in the position

Figure 21 (upper left). Male spruce grouse strutting on a branch.

Figure 22 (upper right). Male spruce grouse approaching female study skin in strutting position.

Figure 23 (lower left). Male spruce grouse showing tail-flicking while walking.

Figure 24 (lower right). Male spruce grouse showing tail-flicking while displaying to female study skin.



described for tail-fanning, was rotated to one side so that the outer retrices of the opposite side were at a right angle to the ground through the plane of the tail. The outer retrices, on the side to which the tail was flicked, were spread, thus accentuating the movement (Figs. 23 and 24).

In the strutting posture the male walked with slow, cautious steps toward and around the female study skin. When walking, tail-flicking was more frequent than tail-fanning (Fig. 23). However, I was unable to correlate the side to which the tail was flicked with which leg was being moved forward. When the male stopped walking, flicking and fanning occurred in no apparent order.

Head-jerk. The head-jerk display has been described by Lumsden (1961a) for the Ontario spruce grouse. Two separate head-jerk patterns were performed by C. c. franklinii. They are the slow head-jerk and the rapid head-jerk. The slow head-jerk display was alternated with strutting around the female. At varying intervals the male stopped, faced either her side or front, and, continuing to flick and fan his tail, jerked his head from one side to the other pausing first with the head to one side than with it to the other (Fig. 25). The position of the head varied from forward, just above the line of the body, to upright, perpendicular to the ground. The bird performed this display for periods of up to 10 seconds. He then strutted around the female again, stopped, and head-jerked from a different angle.

In the rapid head-jerk display, the male faced the female and bent forward bringing his head down close to the ground and his tail up to the perpendicular. He then tossed his head very rapidly from one

side to the other for up to 3 seconds, paused, looked in the direction of the female for 1 or 2 seconds, and then repeated the procedure. The head remained close to the ground during this display. In both the slow and rapid head-jerk display, the bird's brilliant red combs contrasted markedly with his solid black neck and tail which was constantly flicked and fanned. However, I was unable to find a correlation between the side to which the head was moved and the side to which the tail was flicked.

Ground pecking. During periods of courtship display, the male often pecked at the ground with his beak. I was unable to observe whether the bill was open or closed. Lumsden (1961a) described this behavior for the spruce grouse and is of the opinion that this is 're-directed movement' and not 'displacement feeding'. He feels that the male's aggressive drive is dominant and that, lacking the required stimulus from the female, he redirects this aggressive energy to attack inanimate objects.

When pecking at the ground, the male strutted in the manner characteristic of sexual display. The posture of the bird (Fig. 26) closely resembled that which was described for the 'head-jerk' display. The actual pecking involved either one or a series of three or four rapid downward thrusts of the head. Following each series, the bird paused for a variable length of time during which he moved his head, with slow, jerky movements, both up and down and sideways. The general pattern of pecking was the same as that observed during actual feeding except that feeding involved a greater number of pecks per series. One observation of a male picking up a piece of material with his beak and quickly

Figure 25 (upper left). Male spruce grouse performing head-jerk display. Note head is paused to one side in this picture. Study skin is to the right of the male.

Figure 26 (upper right). Male spruce grouse pecking at the ground during courtship display.

Figure 27 (center). Male spruce grouse rushing at female study skin from head-on. Note the full spread of the tail.

Figure 28 (lower left). Male spruce grouse responding to a male study skin with the head and tail-down display. The study skin, behind the male, shows a white breast where the male removed the feathers.

Figure 29 (lower right). Male spruce grouse in upright attack position.

throwing it away suggests that the bird was not actually feeding during this display.

While pecking at the ground, birds occasionally flicked their wings. Both wings were moved rapidly from the slightly drooped position downward and away from the body and back to the starting position. In one instance the wings were flicked once, but in the other three observations of this display they were flicked twice. A similar wing movement was also observed in the 'head-on rush'.

Head-on rush. Lumsden (1961a), in describing this display for Ontario spruce grouse, labeled it 'tail-flick' which I do not follow since this could be confused with other tail movements.

The male, while strutting around the female, would often suddenly rush at her from head-on. He would stop when only a few inches away, fan his tail wide open (180+ degrees), duck his head down, flip his wings open, and utter a barely audible hissing sound (Fig. 27). This display is, perhaps, analogous to the precopulatory hoot of the blue grouse (Dendragapus obscurus) (Brooks, 1926). Since the duration of the rush was very short (less than 1 second) it was impossible to determine any sequence of movements. The bird's feet were not visible in the vegetation and the 'marking time' described in spruce grouse by Lumsden (1961a) was not substantiated.

Mounting. On one occasion the male attempted to copulate with the study skin. The only time he approached the female from the rear was when he tried to mount. In four attempts he was unsuccessful in staying on the female skin's back long enough to copulate. The female was in an upright position and was too wobbly to support him. The male

mounted, in full strutting posture. He grasped the back of the female's neck with his beak and, balancing on his wing tips, attempted to walk up her back.

Aggressive Displays

Lumsden (1961a) noted that males did not respond to mounted male skins and suggested that perhaps artificial combs were needed. Therefore, I placed bright red pieces of felt in the position of the combs and on May 15, 1966, was successful in eliciting aggressive behavior from an adult male. Two postures were observed.

Head and tail-down. The territorial male first responded to the male skin with the display described by Lumsden as 'head and tail-down'. The bird walked with his head, body and tail on the same plane which varied from horizontal to 20 degrees above it. The feathers on his chin were fluffed, giving the appearance of a small beard. The tail was closed and the wings were held close to the body. His neck was held low so that his shoulders appeared hunched. The combs were only half expanded (noticeable but not large) (Fig. 28).

While in this position he walked rapidly, moving his head both up and down and sideways. At varying intervals the bird produced a series of barely audible sounds. Lumsden (1961a) describes these as, "sounding like harsh hissing . . . two calls uttered half a second apart and then five uttered in very quick succession. . . ." C. c. franklinii grouse follows this pattern. The first two sounds were as described. The rapid series of calls, however, were throaty 'kuks'. When the 'kuks' were produced, the beak opened for each, the throat

(below eye and beside white line) pulsated, and the tail flicked up and down. The sounds were only audible for approximately 20 feet.

Upright attack. After circling the study skin a number of times, the bird then approached it from the front. He assumed an upright posture (Fig. 29) with the neck extended upwards and the bill parallel to the ground. The feathers, except those on the chin, were still sleeked. He remained in this position, approximately 1 foot from the skin, for up to 5 seconds. He then leaped at the skin. The tail was fanned, the wings beat strongly, and he pecked at the head and breast of the study skin. Following the attack, which lasted for 1 or 2 seconds, the male resumed the head and tail-down posture and began circling. After circling for a variable length of time, the male again approached from the front and attacked the study skin. The attacks continued even after the male had removed the combs. The male was successful in removing the artificial combs, and the skin and feathers from the neck and upper breast of the mounted bird.

Displays to the Investigator

On a number of occasions resident adult males performed displays which appeared to be directed at me. Two types of displays were observed.

Strutting. The male's posture resembled that observed during the sexual strutting display (p. 56; Figs. 21 and 22) and was performed when a female was near the male. The birds exhibited this many times during the mating season and it was also observed in late summer (August). Birds performed this display only when they were on the ground or in a tree a short distance above it. Birds in trees higher than 20 feet did not display even when a female was near.

This display can best be described as low intensity strutting. When the birds were on the ground, the posture was very similar to sexual strutting except that the head was generally held higher. The amount of neck and breast feather erection varied, but seldom reached the intensity observed in sexual strutting. Birds displaying in trees (Fig. 30) exhibited greater variation in the angle (from 70 degrees to horizontal) and spread (from zero to one-quarter open) of the tail. In some cases the bird only fluffed his neck and breast feathers.

Low intensity strutting also differed from sexual strutting in that the posture was held for a much shorter length of time. A bird, in the normal posture, when approached, would assume a strutting posture in a fraction of a second. He would remain in this position for up to one or two minutes, and then return to normal. The speed of relaxation varied from very fast to 5 seconds. The bird remained in the display posture for longer periods of time when, while at close range, I moved.

Head and tail-down. On three occasions (June 25, 30 and July 6) head and tail-down displays were directed at me by two different males. In all three instances the birds were in trees approximately 15 feet above the ground and the sounds and posture (Fig. 28) were identical to those described in the section on aggressive behavior (p. 63). However, in these cases no upright attack followed the display.

The reason that this display was elicited at these times is unknown. No females were located and none were known to be in the immediate vicinity of the male at the time.

Nesting

In the two years of field work no spruce grouse nests were located. The adult females, in both years, disappeared in late May or early June and did not reappear until early July. In 1966, broody hens were located on July 7 and 8. It was estimated that their chicks (which were measured 1 and 5 days later) were not more than 5 days old when these hens were first seen. From this it is assumed that the nesting season on this study area occurred in June and that hatching took place around the first of July.

One of the hens, which was later located with a brood, was located on June 14 and was assumed to have been nesting at that time. She did not, however, exhibit any unusual behavior.

No evidence of renesting was observed in these birds. In 1966, one female lost her brood at about the age of 10 days. She returned to a male's area and was seen repeatedly thereafter until August 27.

Behavior of Hens with Broods

The behavior of the hens with broods differed markedly from those without. Broodless hens responded to me in the same manner as non-displaying males, remaining quietly in trees while under observation.

The intensity of the response of brood hens varied, first with the age of the chicks, and secondly with my proximity to the chicks. As the age of the chicks increased the intensity of broody behavior exhibited by the hen decreased. One hen with very young chicks (estimated to be less than one week old) was observed in three different situations.

In the first case, the dog had located the brood some distance from me. By the time I arrived, the chicks had dispersed and were

hiding, and the hen had successfully lured the dog away. The hen, sitting in a tree approximately 25 feet above the ground, was clucking softly, with intermittent pauses. If left undisturbed the length of the pauses increased and the amount of clucking trailed off. If, however, I or my dog approached the tree in which she was sitting, she responded with louder, continuous clucking and often moved about on the branches.

The second situation developed when I was close to the brood when it flushed. The hen's initial reaction was loud clucking and flapping of the wings. She then flew (still clucking) in a straight line away from the now scattered brood. The flight was erratic in that she flew close to the ground and gave the appearance of having great difficulty gaining altitude. This behavior was always effective in drawing the dog away from the brood. On a number of occasions I allowed the dog to chase the female immediately after she flushed. Although she appeared to be vulnerable to predators at this time, the dog never came close to catching her. The hen, however, returned to the original flushing site with surprising swiftness. As long as I was in the area she flew from tree to tree clucking loudly and continuously. She often flew to the ground but remained at least 40 feet from the dog and me.

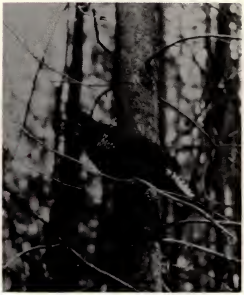
The third form of broody behavior was observed when I captured a young chick. In response to the chick's calls, the hen would actively attack me. However, at no time did she actually make contact with me. She normally responded to the call by flying at me with rapidly beating wings and loud clucking and land on the ground a few feet away. While on the ground she moved constantly and rapidly, approaching as close as 2 or 3 feet and then moving away. When close to me the hen drooped her

Figure 30 (upper left). Male spruce grouse exhibiting low intensity strutting. Note the elevation of the tail.

Figure 31 (upper right). Spruce grouse brood hen reacting to the call of a chick which I was holding.

Figure 32 (lower left). Spruce grouse brood hen remaining in the vicinity of her hidden chicks.

Figure 33 (lower right). Male spruce grouse sitting in a tree in the 'normal' position.



wings until the outer primaries dragged on the ground. Her tail was slightly open and held at about 70 degrees above the horizontal (Fig. 31). When she moved away she usually resumed a normal posture but continued moving and clucking (Fig. 32). A new series of calls from the chick I was holding would bring her rushing in close (either flying or running) once again.

B. Maintenance Behavior

Postures

Normal. Birds were usually found sitting in trees at heights of up to 40 feet. In many cases the birds appeared to be undisturbed or unconcerned by my presence. The posture was the same when I observed them from behind a blind for long periods of time. The bird's posture at these times can be considered 'normal'. The head was erect but the neck was not extended, the bill pointed forward, and the legs were bent so that the belly rested on the feet. No feathers were out of place or fluffed, the wings were held close to the body, and the tail was closed and held in a line with the back (Fig. 33). These birds were probably not sitting tight in order to avoid detection, because they often preened or fed. They frequently flew to the ground which indicated unconcern with my presence.

Alert. The majority of the birds in trees, however, particularly those that were recently flushed, were very much aware of my presence. The bird's general posture was the same as described above except that the head moved considerably. The neck was extended forward and the head was often held as low as the branch upon which the bird was sitting.

The head was turned so that one eye was directed toward me and sideward movements were employed to keep me or my dog in view (Fig. 34). The birds appeared to be more concerned about the whereabouts of the dog than of me.

Birds in trees at heights of over 25 feet were generally unconcerned with my presence. The behavior of the birds was unpredictable when they were between 25 and 15 feet above the ground. Birds below 15 feet were very wary and flushed readily.

Non-displaying birds located on the ground were always in one of two alert postures. In the 'crouched alert', the bird sat on the ground with its head and neck drawn in (Fig. 35). In the other posture, 'upright alert', the bird stood with its head and neck extended upwards (Fig. 36). In both postures the bird's head was cocked so that one eye was fixed on the intruder.

When first approached, the bird was usually in a crouched position. As I slowly moved closer the bird either flushed or assumed an upright posture. If I moved still closer, the bird would walk away in the upright posture and, when far enough away, would resume a crouched posture. If, however, I followed the bird, it would eventually crouch and then fly into a tree.

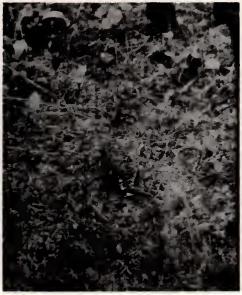
Head drawn back. On occasion birds were observed sitting on limbs in an exaggerated crouched position. The head and neck were greatly pulled back and the breast feathers were slightly raised resulting in the head being posterior to the breast feathers. This posture was commonly seen during inclement weather.

Figure 34 (upper left). Male spruce grouse showing alert posture in a tree.

Figure 35 (upper right). Female spruce grouse in the crouched alert posture.

Figure 36 (lower left). Female spruce grouse in the upright alert posture. Note how the coloration of the female blends with the background.

Figure 37 (lower right). Male spruce grouse running.



Feeding

Birds were observed feeding only on lodgepole pine (Pinus contorta) needles. A bird would walk along a branch, pause, then, with a quick downward thrust of the head, cut off the distal half of the needle with its bill. The resulting sound (a click) was audible up to 50 or 60 feet from the base of the tree in which it was feeding. The birds did not eat all of the needles within reach. Rather, they either purposely or randomly selected a few of the available ones then moved to a new branch or to a new area on the same branch. Generally, the birds spiraled upwards on the tree when feeding.

Panting

On very hot (80-90 degrees F) days birds often panted. The bird would sit or stand on a limb with its neck slightly extended forward and its bill open 3 or 4 mm. at the tip. When the bird panted the chin and upper part of the neck fluttered rapidly. If the sun went behind a cloud the panting ceased, but was resumed when it came out again. When the sun was out for a considerable period, panting was not continuous but sporadic. If, during a pause, I or my dog moved, the bird would immediately begin to pant.

Escape

The spruce grouse is well known for its apparent lack of fear of man and is commonly called the 'fool hen' throughout its range. I found the birds relatively tame but that they were always aware of my presence (p. 69). The tendency to remain motionless when approached is probably an adaptive advantage which is enhanced by their cryptic coloration. Males, viewed from below, have a black and white color pattern which

blends with the clumps of needles against the sky. When observed from above, the male's dark back, mottled with brown, blends well with the shaded ground. The females are a lighter color than the males. Their mottled, light undersides, however, also make them hard to distinguish against the sky. The female's speckled, brown back blends well with most forest backgrounds but is particularly suited for openings and the less dense forest where more sunlight reaches the ground (Fig. 36). It is the combination of protective coloration and behavior that increased the bird's chances of being overlooked by a predator. That such 'foolish' birds survive attests to the fact that they are capable of escaping predation.

Flushing. The bird's most effective means of escaping a ground predator is by flushing. Of the two alert postures shown by the birds when they were located on the ground, only the crouch can be considered a preflight posture. When in the upright position, birds generally walked away and when walking or standing in the upright position they would crouch prior to flying.

Birds in trees also often crouched before flying. Generally an increase in activity (walking, moving head, etc.) preceded flight. However, in many instances birds performed the intention movements and then did not fly.

Birds could be induced to fly by shaking the tree in which they were sitting. An interesting method of evasion was observed when a bird was flushed and appeared to fly a long way. Flying in a straight line, it would gain altitude and fly 80 or 90 yards, circle back and land only 15 or 20 yards from the original flushing site. I was able to relocate

the bird by waiting at the flushing site and listening for it to land. The dog, however, was always fooled by this tactic and was generally unable to relocate them.

In general, males tended to flush more readily than females.

Running. As has been mentioned previously, birds often tried to escape by running, or walking, away from the intruder. When found in the open (i.e., on a road) birds would head for the nearest cover. Curiously enough they crossed the opening with slow cautious steps. Upon reaching the cover they immediately began running. This sequence was also often observed when birds were located in the forest. The bird walked away slowly in the upright alert posture and only began running (if it did not crouch) when it was some 40 feet away. When running, the bird's head, body and tail were on the same plane which varied from 10 to 20 degrees above the horizontal (Fig. 37).

Chicks. Very young chicks (less than one week old) escaped detection by crouching either in the vegetation or under some suitable cover (Fig. 38). After this age, the chicks were able to escape ground predators by flying into trees. When in the trees they sat motionless in a crouched position and were easily caught because they were reluctant to fly (Fig. 39). One chick (approximately 4 weeks old) was located in a tree above the height of the noosing pole. When I shook the tree (which never failed to flush the adults) the chick actually fell down to the limb below. I repeated this until it reached noosing height. When released, it flew strongly.

Figure 38. Spruce grouse chick (arrow) hiding under the vegetation.

Figure 39. Spruce grouse chick sitting in a tree.

SUMMARY AND CONCLUSIONS

The purpose of this investigation was to initiate a study of the breeding biology of the spruce grouse (C. c. franklinii) in Northwestern Montana. The study was conducted on a 600 acre area 30 miles north of Columbia Falls, Montana. Data were collected during the spring and summer (April-September) of 1965 and 1966.

A dog (English pointer) was used to locate grouse, which were captured by noosing, and individually marked with leg bands. The sexual dimorphism of the plumage permitted sexing of the adult and subadult birds. The primary remiges were used to divide the grouse into two age classes: adults, birds two years old and older; and subadults (= yearlings), birds hatched the previous year. The two outer primaries (9 and 10) of the yearling birds are more pointed and often of a lighter color than the other primaries. The primaries are uniform in appearance in the adult birds. In addition, it was found that the total length and color of the removed central rectrix were useful as aging criteria.

The overstory vegetation consisted entirely of lodgepole pine (Pinus contorta). The study area was divided into three zones according to the density of the lodgepole pine: open, not exceeding 2500 stems per acre; medium, 2500 to 5000 stems per acre, and thick, over 5000 stems per acre.

In 1965, the breeding population of spruce grouse on the 600 acre area consisted of four adult males and three adult females. In 1966, five adult males and two adult females resided on the area. In

both years the resident spring population was composed of adult birds only and all adults were residents. The density of five territorial males per square mile is comparable to the spring density of territorial males (six per square mile) in Alaska (Ellison, personal communication).

Four of the adult males were residents on the area during both years of the study. These birds were restricted to home ranges that varied in size from 10 to 15 acres. The birds occupied the same home ranges in both years. A male banded as a yearling in 1965 was a resident in 1966. This new home range was in an area formerly unoccupied by resident males and was only 3 acres in size.

During the spring (April and May), the males occupied breeding territories within their home ranges. Following this period, their movements increased and they utilized a greater portion of their home range.

The male home ranges contained parts of the 'medium' and the 'thick' lodgepole pine zones. The breeding territories were in the 'medium' zone and the 'thick' zone was utilized following breeding. Males were never found in the open zone.

The three adult females located in 1965 occupied home ranges that were coincidental with the home ranges of three resident males. The females moved more extensively than the males and occupied almost all of the available habitat in 1965. The loss of one female the following year did not alter the home ranges of those remaining.

Females with broods occupied areas that were distinct from their general home ranges. The major difference between the areas was the vegetation. The home ranges were in the 'medium' to 'thick' lodgepole

pine zones while the brood ranges were in the 'open' zone. Only hens with chicks were found in the 'open' zone.

The yearling birds traveled extensively during the early part of the breeding season. Late in the season they restricted their movements to previously unoccupied areas and appeared the following spring as territorial adults.

Adult and yearling males showed no seasonal weight change from may to September. The females, however, were heavier in May and June than in July and August.

Molting of the primaries began around the first of June and was completed by the third week of September. The males of both age classes began molting one or two weeks prior to adult and subadult females. Replacement of the rectrices began after the second week of July and was usually completed by the end of August. The young of the year completed their postjuvenile primary molt (juvenile primaries 9 and 10 were retained) by the end of September.

The late fall, winter and early spring diet of the grouse consisted almost entirely of lodgepole pine and other conifer needles. Herbaceous vegetation and insects were utilized during the summer months.

Territorial males performed three basic displays during the mating season (mid-April to mid-May). Flight display consisted of a male flying from a tree to the ground. When he was approximately 4 feet above the ground, he checked his downward flight, rotated his body to a vertical position, and dropped straight to the ground producing two loud sounds. This display has been called 'wing-clapping' and is a variation of the 'flutter-jump' (Lumsden, 1961a) of the other spruce grouse subspecies. Possible factors controlling the occurrence of wing-clapping

include the internal state of the bird, a disturbance from the environment, temperature, cloud cover, and time of day. Probable functions of this display are territorial advertisement, advertisement of their internal reproductive state, and attraction of females.

Courtship behavior was elicited from a male by placing a mounted female skin in his territory. Basically, the courtship displays were the same as described by Lumsden (1961a) for the Ontario spruce grouse. One minor difference was noted in the 'head-jerk' display. C. c. franklinii performed two separate patterns of this display. In the slow head-jerk the male jerked his head from one side to the other, pausing first with it to one side then with it to the other. In the rapid head-jerk he tossed his head rapidly from one side to the other, without pausing, for up to 3 seconds.

The aggressive behavior, elicited by a mounted male study skin placed in a territory, was also similar to what Lumsden (1961a) described for the Ontario spruce grouse. One variation was noted. When in the 'head and tail-down' posture the male uttered a series of sounds. The first two were hissing sounds but these were followed by a rapid series of five 'kuks'.

Spruce grouse survive in the remote and semi-remote mountainous areas of Montana. In the proper habitat (dense stands of young conifers) they are capable of escaping predation by a combination of their protective coloration and their behavior. Forest fires and logging are beneficial to the grouse as they provide new optimum habitat. Probably the most detrimental factor to the spruce grouse is the encroachment of civilization.

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